

NEW WORLD JUGLANDACEAE, III. A NEW PERSPECTIVE OF THE TROPICAL MEMBERS WITH WINGED FRUITS¹

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ABSTRACT

Morphological and anatomical evidence is presented for recognizing the generic status of the two American species of Juglandaceae with winged fruits. *Oreomunnea pterocarpa* is endemic to Costa Rica, while *O. mexicana* ranges from Mexico to Costa Rica. *Engelhardia nicaraguensis* Molina is reduced to synonymy under *O. mexicana* subsp. *mexicana*, and *O. mexicana* subsp. *costaricensis* is described as new. Information is provided on the geographic range, general ecology, morphology, and taxonomy of the American taxa. The somatic count of $2n = 32$ for *O. mexicana* subsp. *mexicana* is the first report for the genus.

The New World species of Juglandaceae with winged fruits form an alliance that is recognized by some as the genus *Oreomunnea* (Hjelmqvist, 1948; Leroy, 1951, 1955) and by others as a section of the predominantly Old World genus *Engelhardia* (Candolle, 1914; Nagel, 1914; Standley, 1927a; Manning, 1949, 1959). While four Central American species have been described to date, the paucity of collections, particularly fertile ones, has handicapped critical taxonomic evaluations. *Oreomunnea pterocarpa* Oersted (1856), for example, is represented today by fewer than fifteen flowering and fruiting specimens. And until recently no fruits of *Engelhardia mexicana* Standley (1927a) had been collected since Rovirosa roamed Chiapas, Mexico, in 1891. *Engelhardia nicaraguensis* Molina (1968) is based on two fruiting specimens, but again no information was made available on the important floral characteristics. The fourth species was described by Standley (1940) as *E. guatemalensis* on the basis of several sterile collections, but as Manning (1959) has since pointed out some of the specimens have proved to be *E. mexicana* and *Alfaroa costaricensis*. The residue of Standley's *E. guatemalensis* is by no means well understood. According to Manning (1959) it "... might not be distinct from *Alfaroa manningii*, *A. hondurensis*, or *Engelhardtia pterocarpa*." Fortunately, this puzzle now seems to have been resolved by the discovery of fruiting material at the type locality. *Engelhardtia guatemalensis* Standley is in reality an *Alfaroa*, apparently related most closely to *A. hondurensis* (Williams & Molina, 1970).

¹ Supported by National Science Foundation grants GB-5233X and GB-28525X. The line drawings are the artistry of Susan Carlton Smith and were sponsored by the Duke University Council on Research. I am indebted to several biologists for their information and support in locating trees in the hinterlands of Mexico and Central America: Drs. Arturo Gomez Pompa and Ramón Riba, Mexico; Mr. Antonio Molina R., Nicaragua; and Drs. William H. Hatheway and Lester R. Holdridge, Costa Rica. The initial fieldwork that was conducted in the spring of 1966 was outstandingly successful, due in large part to the support of my research assistant, Mr. Louis F. Conde, and travelling companions, Drs. Marshall R. Crosby and James W. Walker. Appreciation is also noted for services rendered by the curators of the many herbaria that have played such an important part in this study: A, CR, DUKE, EAP, F, GH, IICA, NO, NY, PH, US. Professor William Louis Culberson has kindly provided the Latin diagnosis, and Drs. R. L. Wilbur, B. G. Schubert, and W. E. Manning have been most helpful in suggesting improvements in the manuscript in form and content.

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Since Manning's last report (1959) on the status of the New World *Engelhardias*, several critical collections have become available for study. The purpose of this paper is to reassess the evidence for recognizing the genus *Oreomunnea*, detail new information on the cytology, morphology and distribution of the American species, and discuss the patterns of variation in light of proposed taxonomic changes.

GENERIC CONSIDERATIONS

Oreomunnea Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 3: 33–34. 1856.

Engelhardtia sect. *Oreomunnea* (Oersted) DC., Ann. Sci. Nat. Bot. IV. 18: 36. 1862.

Engelhardtia sect. *Oreomunnea* (Oersted) DC., Podr. 16: 142. 1864.

Oreamunoa Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1870: 166. 1870.

Trees, or rarely large shrubs; bark scaly or tight; pith solid; buds naked; leaves opposite, evergreen; leaflets 4–12, opposite to subopposite, symmetrical to asymmetrical at base, revolute on one or both margins, with or without auricles, with or without serrations on young trees and stump sprouts, entire on mature trees, adaxial surface glabrous, abaxial surface dotted with peltate scales; monoecious, with both staminate and androgynous panicles, in the latter case female spike flanked by 1–3 decussate pairs of staminate catkins; staminate flowers numerous, alternately arranged, abaxial 3-lobed bract cupped or long and slender, receptacle round or elongate, inner floral envelope of 2 bracteoles and 2–4 sepals, stamens 8 in one series to 18 or so in two series, pollen tectate with fine scabrate sculpturing, diameter *ca.* 20 μ ; pistillate flowers numerous, alternately arranged, subtended by 3-lobed abaxial bract and adaxial bracteolar rim, calyx tube fused to bract-bracteole cup at base, forming distinct tube above, deeply parted, with 4 narrow or broad sepal lobes extending to summit of stigma or beyond, style short or long tapering, deep cleft separating two stylar arms, stigmas horseshoe shaped, carinal, capping the ends of the stylar arms; fruit 3-winged, medium to large (5–13 cm), adaxial bracteoles expanded to cover pistil, nut 8-celled at equator; germination hypogeal, first two aerial leaves opposite and simple or compound, succeeding several leaves alternate and simple or compound, shifting to opposite, compound leaves at maturity.

When Oersted described *Oreomunnea*³ (1856) as a new endemic genus from Costa Rica, he was quite aware of its close kinship to the Old World *Engelhardias*. However, he stressed particularly basic differences in the stigmas, fruit, and seed. With little additional information de Candolle (1862) saw fit to reduce the New World taxon to sectional rank in the genus *Engelhardia*. Thus started the long-standing debate on the merits of *Engelhardia* sect. *Oreomunnea* versus *Oreomunnea*. Once the lines were drawn more opinions were added without shedding much additional light. Oersted (1870*a*, 1870*b*) restated the case for recognizing the genus *Oreomunnea* and was later given support by Hjelmqvist (1948) and

³ The name has been spelled in various ways since the genus was first described in honor of don Francisco María Oreamuno. Manning (1949: 200) discussed the tortured history of the spelling in a footnote.

Leroy (1951, 1955); however, de Candolle (1864, 1914), Standley (1927*a*), and Manning (1949, 1959) continued to classify New World Juglandaceae with winged fruits as a section of *Engelhardia*. As Manning (1949) has so aptly pointed out, the decision on what to call the New World group depends on which of many similarities and differences are emphasized.

The issue took on new dimensions as a result of Standley's report (1927*b*) of another new genus, *Alfaroa*, from Costa Rica. Though Standley mistook the superficial similarity of the fruit as a basis for close relationship with *Juglans*, Manning (1938, 1940, 1948), Hjelmqvist (1948), and Leroy (1955) have since established that *Alfaroa* has its closest affinities with *Oreomunnea*. This appears to be a most remarkable assertion, because *Alfaroa* has a wingless fruit, whereas both *Oreomunnea* and *Engelhardia* have a conspicuous 3-winged bract. Manning (1949, 1959) summarized the many similarities of the New World members and presented substantial evidence that the fruit is about the only reliable basis for distinguishing between *Alfaroa* and *Oreomunnea*. The question then becomes one of assessing the relationship of *Alfaroa* and *Oreomunnea* as well as *Oreomunnea* and *Engelhardia*. On the basis "that the only reliable features are the position in flower and the condition in fruit of the bract and bracteoles (prophylls) . . ." Manning (1949) concluded that *Oreomunnea* is best considered a section of *Engelhardia* and that *Alfaroa* should be recognized as a weak generic segregate. Since the last reappraisal, however, new data on leaf crystals (Stone, unpublished) and seedlings (Conde & Stone, 1970; Stone, 1970), when combined with previous findings on phyllotaxy, venation patterns, and fruit morphology, provide, in my view, persuasive evidence for conferring generic rank on *Alfaroa*, *Oreomunnea*, and *Engelhardia*. The essence of these findings is summarized in Table 1 and discussed below.

Five characters shared by *Alfaroa* and *Oreomunnea* seem particularly significant in focusing on the close relationship of these New World members of the family. (1) Phyllotaxy is opposite at maturity (Figs. 2A, 7A; Stone, 1968: Fig. 1), though both genera pass through the seedling stage with alternate leaves (Figs. 4F, 9G; Stone, 1968). Occasionally, however, the phyllotaxy may vary between alternate, opposite, and whorled in rapidly growing shoots of *Alfaroa*. Members of both Old World sections of *Engelhardia* (§ *Engelhardia* and § *Psilocarpeae*) possess alternate phyllotaxy throughout their life span (Jacobs, 1960; Manning, 1966). (2) The intercostal and marginal leaf-venation patterns which permitted Wolfe (1957) to make generic identification of extant and fossil Juglandaceae are useful in recognizing two groups. *Alfaroa* and *Oreomunnea* form part of one group which is characterized by an intercostal network of closed veinlets. The second group, in which *Engelhardia* is a member, has an intercostal mesh that forms a network of free-ending veinlets. (3) Leaf crystals also serve to identify the Old World and New World components. As Nagel (1914) and Metcalfe and Chalk (1950) have pointed out, calcium oxalate crystals are common in various tissues of the juglandaceous plant. Leaf crystals in particular are common in certain genera and are often quite conspicuous. In hickories (*Carya*), for example, the adaxial leaflet surface may show minute bumps which are caused by druse crystals in the palisade parenchyma. A survey of leaf crystals indicates that druses are

TABLE 1. Diagnostic features of *Alfaroa*, *Oreomunnea*, and *Engelhardia*.

CHARACTER	<i>Alfaroa</i>	<i>Oreomunnea</i>	<i>Engelhardia</i>	
			§ <i>Psilocarpeae</i>	§ <i>Engelhardia</i>
Phyllotaxy	opposite	opposite	alternate	alternate
Leaflet venation, intercostal mesh	closed veinlets	closed veinlets	free-ending veinlets	free-ending veinlets
Leaflet crystals, large rhombic	present	present	absent	absent
Fruit size	large	medium	small	small
Fruit partitions	8-celled	8-celled	4-celled	2(–4)-celled
Position of cotyle- dons in fruit	separate	separate	tangled	tangled
Testa of cotyledons	tight	tight	loose	loose
Seedling germination	hypogeal	hypogeal	epigeal	epigeal
Cotyledonary node	1-gap, 3-trace	1-gap, 3-trace	1-gap, 2-trace	1-gap, 2-trace
Pollen diameter (μ)	24 (19–29)	21 (19–23)	15 (13–17)	19 (15–25)
Pollen, polar view	subtriangular	subtriangular	triangular	subtriangular
Pollen, equatorial view	suboblate	suboblate	oblate	oblate-spher.
Pollen nexine	thick	thick	thick	thin
Stigma orientation	carinal	carinal	split-carinal	commissural
Stigma shape	subglobose	subglobose	subglobose	elongate
Inflorescence	terminal and lateral	terminal and lateral	terminal and lateral	lateral
Fruit bract	very small	3-winged	3-winged	3-winged
Fruit bracteoles	very small	large	small	small
Fruit wing venation	absent	triveined	pinnate	pinnate

common in *Carya*, *Juglans*, *Pterocarya*, and *Platycarya*, but not in *Alfaroa*, *Oreomunnea*, or *Engelhardia*. Instead, *Alfaroa* and *Oreomunnea* have numerous small crystals in the leaf struts formed by the bundle-sheath extensions and large rhombic crystals localized primarily in the palisade. Large rhombic crystals have not been detected in *Engelhardia*. (4) The internal anatomy of the fruit of *Alfaroa* and *Oreomunnea* is also distinctive. A median cross section of the fruit exposes eight chambers in these New World genera (Figs. 4E, 9F; Stone, 1968: Fig. 13) but only two or four in *Engelhardia* (Leroy, 1955; Manning, 1966). The basic partitioning of the fruit into two chambers is effected by the primary septum. Primary and secondary septa intersect to form the 4-chambered fruit, while the 8-chambered condition is the result of the elaboration of tertiary septa which bisect each of the four basic chambers. Leroy (1951, 1955) also discovered that the vascularization of the fruit is identical in *Alfaroa* and *Oreomunnea*. Four placental strands fuse into one bundle in the plane of the primary partition prior to entering the funiculus. In *Engelhardia*, on the other hand, there are only two placental strands present to unite into a single vascular bundle. (5) The morphology of junglandaceous seeds and seedlings is a subject of considerable import and has been detailed elsewhere (Conde & Stone, 1970; Stone, 1970). The main findings confirm the separation of *Oreomunnea* from *Engelhardia* and its alliance with *Alfaroa*. *Engelhardia* has epigeal germination and one-gap, two-trace cotyledonary nodes. *Oreomunnea pterocarpa* (Conde & Stone, 1970: Fig. 7) and *O.*

mexicana (Fig. 9G) are hypogeal and have a one-gap, three-trace cotyledonary node as in *Alfaroa* (Conde & Stone, 1970: Fig. 20). While I was surprised to discover that the New World taxa with winged fruits have hypogeal germination, Hjelmqvist (1948: 58) shrewdly observed that the testa "attaches itself to all irregularities of the cotyledons, while in *Engelhardtia* it forms an even covering. *Oreomunnea* in this respect approaches the type that is found in *Juglans* and *Carya*, the character possibly being connected with the fact that the germination is hypogeal as in these; the germination of *Oreomunnea* is, however, not described."

The similarities of *Alfaroa* and *Oreomunnea* as discussed above are subtle but quite substantial. The similarities of *Oreomunnea* and *Engelhardtia* are more apparent than real. By this I mean that the conspicuous 3-winged fruits that are common to both taxa are, on closer examination, quite distinctive. As the paleontologists have long recognized and MacGinitie (1969) recently commented, *Oreomunnea* fruits have a 4-lobed involucre consisting of 3 wings (bract) and a well developed adaxial or basal lobe (bracteoles) that covers the pistil. *Engelhardtia* on the other hand has a 3-winged involucre with a highly reduced fourth lobe. Furthermore, the wings are triveined with looping laterals in *Oreomunnea*, whereas *Engelhardtia* wings have pinnate venation. The closest ties of *Oreomunnea* to *Engelhardtia* are through *E. roxburghiana* (Leroy, 1955; Stone, 1970), a monotypic representative of sect. *Psilocarpeae*. Whitehead (1965), for example, viewed the small, triangular pollen grains of *E. roxburghiana* as similar to an ancestral type from which were derived the larger subtriangular grains of *Alfaroa*, *Oreomunnea*, and *Engelhardtia* sect. *Engelhardtia*. The intermediate status of *E. roxburghiana* is further supported by similarities to *Oreomunnea* in inflorescence position, stigma orientation, fruit anatomy, and staminate flower morphology. Both taxa, as well as *Alfaroa*, have terminal androgynous panicles from which specialized lateral inflorescences were derived (i.e. *E.* sect. *Engelhardtia*; Manning, 1938). Stigma development and orientation, a feature that has undergone considerable change in the evolution of the family (Manning, 1940), also characterizes *E. roxburghiana*, *Oreomunnea*, and *Alfaroa*. The short style and stigma are bifurcate with the primary separation oriented parallel to the line of carpel fusion, i.e. carinal stigma (Manning, 1940; Leroy, 1955: Fig. 75). The secondary or minor separation that is oriented at right angles to the primary separation is quite pronounced in *E. roxburghiana* and effectively separates the stigma into four lobes, hence giving rise to the term split-carinal. The more specialized members of *Engelhardtia* have commissural stigmas with the elongate stigma halves positioned at right angles to the line of carpel fusion. As mentioned previously, *Alfaroa* and *Oreomunnea* have 8-celled flowers and fruits, whereas those of *Engelhardtia* are either 2- or 4-celled. The fruits of *E.* sect. *Engelhardtia* are 2-celled at the equator, although a weakly developed secondary partition is frequently present at the base. *Engelhardtia roxburghiana* flowers are fundamentally similar to *Oreomunnea* but have a much more simple organization (Leroy, 1955). They lack the tertiary partition altogether, and the secondary partition is only moderately well developed. In addition, however, Leroy notes that the development of a *excroissance tabulaire* at the plane of insertion of the ovule

in *E. roxburghiana* (Leroy, 1955: Fig. 72) establishes a relationship with *Oreomunnea* (and *Alfaroa*), as well as with *Pterocarya* (and *Platycarya*). The staminate flowers are somewhat less revealing of relationship, although *E. roxburghiana* and *Oreomunnea mexicana* (Figs. 7D, E) are the only members of the complex with a regularly arranged floral envelope. Manning (1948) notes, for example, that "In all species of the genus except *E. chrysolepis* [*E. roxburghiana* Wall.] the bracteoles and lateral sepals may be irregularly arranged so that it is often difficult to determine the exact identity of a given organ." The male flowers of *Oreomunnea pterocarpa* more closely approximate the irregular floral envelope arrangement found in *E. sect. Engelhardia*.

Even after the last character is assessed in the evaluation of relationships, the decision as to the appropriate taxonomic rank to assign a particular taxon remains in the subjective hands of the taxonomist. The evidence presented here leads me to conclude that the ties between *Alfaroa* and *Oreomunnea* are just as strong as those between *Oreomunnea* and *Engelhardia*. Consequently, it would seem logical that the three taxa should be given coordinate rank; whether it be at the sectional or generic level depends, of course, on their standing in relation to the other members in the family. In this regard Manning (1949) has stated that *Alfaroa* is as distinct from *Engelhardia* as *Juglans* is from *Pterocarya*. Accepting this opinion I must conclude that *Alfaroa*, *Oreomunnea*, and *Engelhardia* deserve generic rank. The dilemma posed by these three taxa reflects a close and what appears to be almost linear relationship. *Engelhardia* sect. *Psilocarpeae* has intermediate characters linking the wind-dispersed members of *E. sect. Engelhardia* and *Oreomunnea*. A shift in adaptive zones from wind to animal dispersed seeds, with the concomitant loss of wings and enlargement of seed, seems like a plausible explanation for the evolution of *Alfaroa* from *Oreomunnea*-like ancestors (Stone, 1970).

SPECIES CONSIDERATIONS

Three taxa of New World Juglandaceae with winged fruits are herein recognized. *Oreomunnea pterocarpa* is endemic to mid-elevations in the central cordilleras of Costa Rica. *Oreomunnea mexicana* (*Engelhardtia mexicana* Standley) is a premontane rainforest element ranging from southern Mexico to Costa Rica. The trees from Mexico, Guatemala, and Nicaragua (*E. nicaraguensis* Molina) are treated as *O. mexicana* subsp. *mexicana*, while the Costa Rican plants are placed in a new subspecies, *O. mexicana* subsp. *costaricensis*. The following section is devoted to a taxonomic appraisal of these taxa.

KEY TO SPECIES OF *OREOMUNNEA*

- Bark tight; shoot tip glaucous; petioles long (3.5–6 cm), hairy at base; petiolules long (5–15 mm); leaflets long (8.5–16 cm), and wide (3–6 cm), sometimes revolute at base but not auriculate, the secondary veins not conspicuously forking; female flowers with elongate style and deep cleft separating styler halves; male flowers with elongate receptacles bearing 16–19 stamens in two disorganized series; fruits large, the lateral wing span wide (to 13 cm); first pair of aerial seedling leaves simple — 1. *O. pterocarpa*
- Bark exfoliating; shoot tip bronzy-yellow; petioles short (1.3–3.3 cm), glabrous at base; petiolules short (to 3 mm); leaflets long (6–10 cm), and narrow (1.5–2.5 cm), revolute and at least some auriculate at base, the secondary veins conspicuously forking; female flowers with short, nearly obsolete style, and shallow cleft demarcating



FIGURE 1. Tree of *Oreomunnea pterocarpa* with 27 in dbh at Stone 2684 location east of Tuís, Costa Rica.

stylar arms; male flowers with small oval to rectangular receptacles bearing 8–12 stamens in one or two series; fruits medium, the lateral wing span narrow (to 5 cm); first pair of aerial seedling leaves compound 2. *O. mexicana*

1. ***Oreomunnea pterocarpa*** Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 3: 33–34. 1856. (Tree: Figs. 1, 2A–C. Inflorescence: Fig. 3;

Manning, 1938: Figs. 9, 20; Hjelmqvist, 1948: Fig. 8C. Staminate flower: Figs. 4A–C; Candolle, 1914: Fig. I; Manning, 1948: Figs. 38–41, 64, 68, 72. Pistillate flower and fruit: Figs. 3, 4D–E; Candolle, 1862: Fig. 50; Oersted, 1870a: Plate II, Figs. 1–11; Eichler, 1878: Fig. 15M; Candolle, 1914: Fig. II 1–3; Manning, 1940: Figs. 32, 33, 61, 78, 102, 103; Hjelmqvist, 1948: Fig. 21a; Pittier, 1957: Fig. 20. Seedling: Fig. 4F; Conde & Stone, 1970: Fig. 7).

Engelhardtia pterocarpa (Oersted) Standley, Trop. Woods 12: 15. 1927.

Tree to 46 m tall, 73 cm dbh (Stone 2222), buttresses well developed; bark tight, outer surface grayish to reddish and verrucose, inner bark yellowish-orange; wood white throughout, with definite growth rings (Heimsch & Wetmore, 1939), diffuse porous, the vessel members from trunk averaging $221\mu \times 937\mu$; pith solid; buds naked, protected by closely appressed, paired leaf-primordia, studded with butter-yellow peltate scales, without hairs, the axillary buds superposed; leaves decussate; petioles 3.5–6.0 cm, hairy at base in sapling and sucker sprouts; rachis 7.0–10.0 cm; leaflets 6–8, opposite to subopposite; petiolules 5–15 mm; blades of leaflets 2.5–3 times longer than wide, 8.5–16.0 cm \times 3.0–6.0 cm, symmetrical to asymmetrical at base, most revolute on one or both margins, most pronounced on basiscopic side, the margins entire, the secondary veins not conspicuously forked; young leaflets pink to greenish yellow; mature leaflets coriaceous, the adaxial surface dark green and essentially glabrous, the abaxial surface light green to glaucous, dotted with peltate scales of two sizes, moderate number of large butter-yellow scales and numerous small transparent or brownish scales, no hairs. *Inflorescences* borne laterally on old wood or occasionally at junction of old and new wood; “androgynous panicle . . . , with usually four to six opposite staminate catkins, the inflorescence terminated by a fifteen- to twenty-flowered pistillate catkin” (Manning, 1938; diagrammed as terminal in Hjelmqvist, 1948: Fig. 8c). *Staminate flowers* alternately arranged; abaxial bract 3-lobed, long and narrow; mature flower with elongate receptacle; inner floral envelope of two bracteoles and 3–4 sepals; stamens ca. 19, in two disorganized series, filaments essentially obsolete, anthers glabrous, dehiscing by longitudinal slits; pollen tectate with fine scabrate sculpturing, suboblate, subtriangular in polar view, pores equatorial, averaging 21μ in diameter. *Pistillate flowers* small (6–7 mm), highly reduced, lacking petals; subtending hand-like cup formed from 3-lobed abaxial bract and adaxial bracteole rim; calyx tube tightly fused to bract and bracteoles, the four narrow sepal lobes appearing as distinct outgrowths of ovary, seemingly not united into calyx tube; ovary inferior, elongate tapering style extending to same height as divergent sepal lobes, with deep cleft separating two stylar arms; stigmas carinal, subglobose or horseshoe shaped, capping ends of stylar arms, verrucose

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FIGURE 2. Vegetative aspects of *Oreomunnea*.—A. Shoot of *O. pterocarpa* displaying decussate phyllotaxy (Stone 1907), $\times 0.4$.—B. Pubescent node of sapling of *O. pterocarpa* (Stone 2169), $\times 1.7$.—C. Leaflet of *O. pterocarpa* (Stone 1907) with secondary veins that curve upward toward tip and end without conspicuous branching, $\times 0.6$.—D. Leaflet of *O. mexicana* subsp. *costaricensis* (Stone 2680) with auricles at base and secondary veins that curve upward toward tip, branch and then fuse near margin, $\times 0.8$.



stigmatic surface confined to rim and outer surface. *Fruits* large, 3-winged, lateral wing spread to 13 cm, central wing to 11 cm long, strong central primary vein flanked by two subordinate primaries and interconnected by looping laterals; adaxial pair of fused bracteoles enclosing globose nut and stylar-stigma region; nut 8-celled at equator, 4-celled near poles; fruit splitting loculicidally along secondary partition on germination. *Seedling* with long, slender tap root; germination hypogeal; first two aerial leaves opposite and simple, succeeding several leaves alternate and simple, followed by transition to compound, and later abrupt shift to opposite phyllotaxy; shoots pale to vivid pink; simple leaves with long petioles (20–30 mm) and large blades (40–80 × 75–250 mm), with conspicuous midrib and secondaries; transitional compound leaves (3-, 5-, and 7-foliolate) with extremely long petioles (30–60 mm), near-sessile lateral leaflets (to 2 mm), and an extended petiolule (15–20 mm) supporting large terminal leaflet (50–100 × 100–200 mm); leaves with more than five leaflets have even-pinnate pattern characteristic of those of mature tree; simple leaves and leaflets of compound leaves entire, no evidence of inrolling of basal margins; adaxial leaflet surface dark green, glabrous; abaxial leaf surface glaucous, free of hairs, dotted with large butter-yellow peltate scales and numerous brown peltate scales.

Oersted's original description (1856) and subsequent discussions (1870*a*, 1870*b*) were based on fruiting material only. It was nearly sixty years before collections by Adolfo Tonduz made vegetative and flowering specimens available for study (Candolle, 1914). The paucity of collections is as much a function of the difficulty of collecting specimens from these forest giants as it is locating them along the steep ravines of the valley and tributaries of the Río Reventazón. Trees in the virgin rainforest around Platanillo and Tuís commonly have plank buttresses extending eight feet in diameter at the base and tapering to a 2 to 3 foot trunk at head height (Fig. 1). The bark is smooth and tight, and the trunk is often without branches for the first 40 to 50 feet. The mature trees may reach 46 m (Tonduz *in de* Candolle, 1914) to become upper story emergents. Young shoots are usually vivid pink, while mature leaves are dark green above and glaucous below. Perceptive native guides are remarkably accurate in spotting the broad crowns from distant hillsides. In the Platanillo area woodsmen readily differentiate between *gavilán blanco* (*Oreomunnea pterocarpa*) and *gavilán colorado* (*Alfaroa manningii* León).

One of the most intriguing aspects about *Oreomunnea pterocarpa* is its highly restricted range. As both Standley (1927*a*, 1937) and Manning (1959) have pointed out, it is known only from the low to middle elevations on the Atlantic drainage of Costa Rica. All of the verified specimens are from the Río Reventazón valley in Cartago Province, although Mr. Charles Lankester presented me with typical *O. pterocarpa* fruits, ostensibly collected at Laguna Hule in Alajuela Province. Collection data from herbarium sheets indicate that *O. pterocarpa* ranges from 200 m (Manning, 1959: locality not cited nor known to me) to 1500 m elevation (Tonduz *in de* Candolle, 1914: Rincón del Indio). The large tree on the grounds of the IICA at Turrialba (Stone 1346) is situated at 550 m, while León's topotype collection from La Gloria (León 1523) was located at 820 m. There is,



FIGURE 3. Inflorescence of *Oreomunnea pterocarpa* (Stone 1346) with laterally borne fruits, $\times 0.54$.

in addition, a cultivated tree in the Botanic Garden of the Universidad de Costa Rica in San José (1168 m) that appears to be doing quite well. Manning (1959) suggested that a specimen from Baja Verapaz, Guatemala (Standley 90967, GH) might be *O. pterocarpa*. However, the specimen is sterile and lacks the glaucous shoot tip and long petiolules characteristic of *O. pterocarpa*; it appears to be a member of the genus *Alfaroa*, probably *A. guatemalensis* (Standley) Williams & Molina.

Oreomunnea pterocarpa, like so many of the tropical forest trees, may be

locally abundant but not common. This is one of the puzzling aspects of tropical diversity that has led to speculation that many tropical plants are self pollinated (Baker, 1959, 1963). *Oreomunnea* has typical amentiferous catkins, and the large 3-winged fruits of *O. pterocarpa* (Fig. 3) show obvious adaptations to wind dispersal. Furthermore, the tree crown is favorably situated in the upper canopy. Fruit production on the tree in San José (Stone 1016) offers affirmative evidence for self pollination in *O. pterocarpa*. No other trees are known to occur within 20 miles of this specimen and yet fruit and seedlings are produced at least occasionally (Jan 1962, Nov 1967).

COSTA RICA. ALAJUELA: Edge of Laguna Hule, ca. 12 km N of V. Poás, no date, *Lankester* (DUKE). CARTAGO: Juan Viñas, no date, *Calvert* 57 (PH); Cachí, Jun 1910, 4 Jul 1914, *Lankester* (NY); La Gloria, bordes del Río Chiz, 820 m, 23 Apr 1949, *León* 1523 (EAP, IICA); La Gloria, 700–800 m, 29 Apr 1914, *Tonduz* 18000 (A, CR, EAP, F, GH, NY, PH, US); Peralta, 13 Jul 1923, *Stevens* 468a (US); grounds of Inst. Interamericano Ciencias Agrícolas (IICA) near Río Turrialba, 550 m, 7 Sep 1949, *León* 1819 (IICA); slope behind IICA station overlooking Río Reventazón, 550 m, 22 Jan 1963, 28 Mar 1966, 26 Jan 1968, *Stone* 1346 (DUKE, NO), 8 Jul 1965, *Stone* 1908 (DUKE); on peninsula between Molina Quebrada and Río Reventazón near Turrialba, 10 Jul 1965, *Stone* 1919, 1920, 1921 (DUKE), 23 Apr 1966, *Stone* 2169 (DUKE); Pejibaye, 2000 ft., 3 Jul 1928, *Stork* 2808 (F); hills S of Platanillo, 22 Jan 1963, *Stone* 1347, 1348 (DUKE); midslopes SE of Platanillo, 25 Mar 1967, *Stone* 2222 (DUKE); Montaña Baja Coronó, E of Tuís and N of Platanillo, 2 Sep 1968, *Stone* 2684 (DUKE); no locality, 1927 and 1964, *Lankester* (F, US). SAN JOSE: Botanic Garden, Universidad de Costa Rica, San José, 3800 ft., 19 Jan 1962, 7 Jul 1965, *Stone* 1016 (Duke), 10 Nov 1967, *Stone* 1016 A, B, C (DUKE).

2. ***Oreomunnea mexicana*** (Standley) Leroy, Bull. Mus. Hist. Nat. (Paris) Sér. 2. 23: 127. 1951. (Tree: Figs. 5, 6A–C, 7A, 8. Inflorescence: Figs. 7B, 7C, 9A, 11. Staminate flower: Figs. 7D, 7E, 10A, 10B. Pistillate flower and fruit: Figs. 9A–F, 10C–J; Manning, 1940: Figs. 34, 35, 106. Seedling: 9G.)

Engelhardtia mexicana Standley, Trop. Woods 12: 15. 1927.

Engelhardtia nicaraguensis Molina, Fieldiana Bot. 31: 358. 1968.

Tree to 32 m tall (*Stone* 2177B) or more, 150 cm dbh (*Stone* 2807 locality), buttresses developed on both downhill and uphill sides of trunk, occasionally extending to height of 3 m; bark exfoliating, outer surface reddish brown, inner bright orange; wood white throughout or heartwood sometimes pink, diffuse porous, the vessel members from trunk averaging $160\mu \times 693\mu$; pith solid; buds naked, protected by closely appressed paired leaf-primordia, studded with bronzy-yellow peltate scales, without hairs, axillary buds superposed; leaves decussate, petioles 1.3–3.3 cm, with dense covering of short hairs (.04 mm) on young trees, rachis 1.8–11.8 cm, with dense covering of short hairs on young trees; leaflets 4–12, opposite to subopposite; petiolules 0–3 mm; blades of leaflets 4–5 times longer than wide, $6.0\text{--}10.0 \times 1.5\text{--}2.5$ cm, symmetrical to asymmetrical at base, revolute on one or both margins, most pronounced on basiscopic side, auricles often present on one or both margins, the margins mainly entire, with coarse serrations on distal half of stump sprouts and some shoots, the secondary veins conspicuously forked; young leaflets pink; mature leaflets coriaceous, the adaxial surface dark green and essentially glabrous, the abaxial surface light green to glaucous, dotted with peltate scales of two sizes, moderate number of large bronze scales and numerous small brownish scales, short hairs on basal portion of midrib

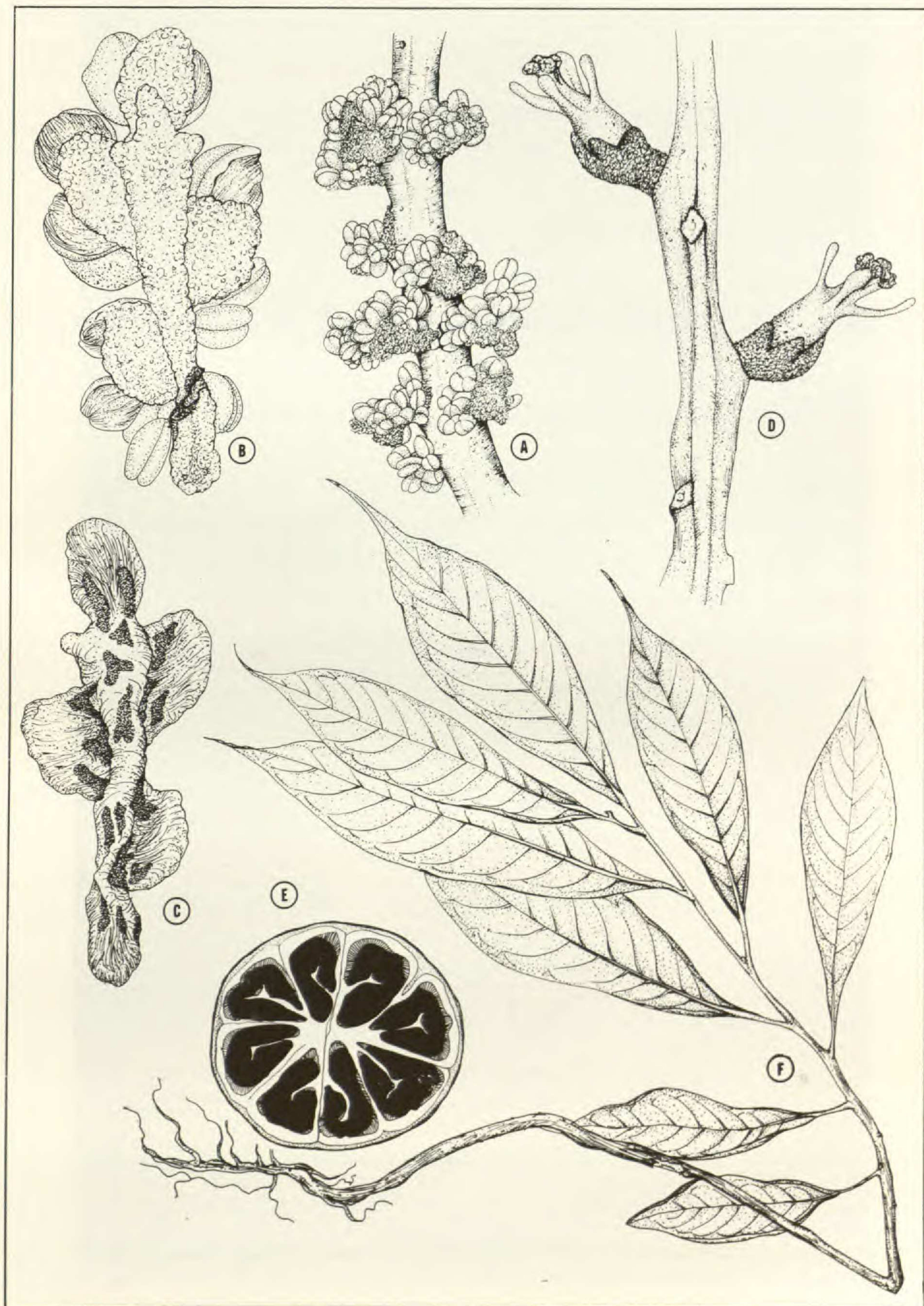


FIGURE 4. Flowers, fruit, and seedling of *Oreomunnea pterocarpa*.—A. Portion of staminate catkin (Stone 1346), $\times 4.3$.—B. Abaxial view of staminate flower with 5 floral segments (Stone 1346), $\times 10.4$.—C. Adaxial view of same flower as in C, exposing attachment points of 19 stamens, $\times 10.4$.—D. Pistillate flowers (Stone 1346), $\times 3.4$.—E. Transverse section of fruit at equator, oriented with primary partition in east-west direction: 8-celled, thin husk and thin cartilaginous shell (Stone 1346), $\times 2.1$.—F. Seedling with alternately arranged leaves, hypogeous cotyledons shed (Stone 2684), $\times 0.4$.



FIGURE 5. *Oreomunnea mexicana* (Stone 2718), 30.5 in. dbh, Tapantí, Costa Rica.

and long hairs tucked in fold of auricle on young trees. *Inflorescences* initiated terminally with flush of new growth or occasionally laterally, of three types: androgynous panicle with central female spike flanked at base by 1 to 3 decussate pairs of staminate catkins (Fig. 11); staminate panicle consisting of 1 to 3 de-



FIGURE 6. Habit and habitat of *Oreomunnea mexicana*.—A. Moderate development of buttresses, Stone 2177B location.—B. Bark separating into long platelets on 14 in. dbh trunk, Stone 2181.—C. Fog-shrouded mountains south of Muñeco, Costa Rica, ca. 1500 m elev., June 1970.

cussate pairs of catkins; pistillate panicle of one to several catkins, fruiting spikes elongate but fruits congested. *Staminate flowers* alternately arranged, small (2–3 mm), sessile or essentially so, outer surface sprinkled with butter-yellow and transparent peltate scales; abaxial 3-lobed bract cupped; mature flower with rounded receptacle; inner floral envelope of two lateral bracteoles and two (rarely three) sepals; stamens 8 in one series, ranging to 12 in two series, filaments essentially obsolete, anthers glabrous, dehiscing by longitudinal slits; pollen tectate with fine scabrate sculpturing, suboblate, subtriangular in polar view, pores equatorial, averaging 19μ (Stone 2144) to 23μ (Stone 2181) in diameter. *Pistillate flowers* small (3–5 mm), highly reduced, lacking petals; subtending hand-like cup formed from 3-lobed abaxial bract and adaxial bracteole rim; calyx tube fused to bract and bracteoles at base, forming distinct calyx tube above, four broad sepal lobes incurved or spread, extending well beyond stigma; style short tapering, with deep cleft separating two stylar arms; stigmas carinal, subglobose or horse-shoe shaped, capping the ends of stylar arms, the verrucose stigmatic surface confined to rim and outer surface. *Fruit* medium-sized, 3-winged, with lateral wing spread to 5 cm, central wing to 4 cm long, with three primary veins and looping laterals; adaxial bracteoles enclosing globose nut and stylar-stigma region, to 12 mm long; nut 8-celled at equator, 4-celled near poles; fruit splitting loculicidally along secondary partition on germination. *Seedling* with long, slender tap root; germination hypogeal; first two aerial leaves opposite and pinnately compound, succeeding several leaves alternate and compound, abrupt shift to opposite phyllotaxy in young sapling stage, 1–2 feet tall (Stone 1872); shoots pale to vivid pink; most leaves odd-pinnate, the 18–20 (14–22) leaflets coarsely serrate; petiole short (to 7 mm) in first formed leaves, longer (to 25 mm) in later ones; leaflets essentially sessile with petiolules rarely 2 mm long; later formed leaflets becoming entire, the last formed leaves of 3–4 foot saplings with entire margins on basal half of leaflets, coarse serrations on distal half; leaflet bases often asymmetrical, auricles usually present on leaflets of larger saplings; a coating of short (.04 mm) hairs on stem tip, petiole, and rachis and a cluster of longer hairs (.6 mm) at junction of petiole and stem; adaxial leaflet surface dark green, with butter-yellow scales scarce; abaxial leaflet surface light green to glaucous, occasionally with a few long hairs at base, dotted with large butter-yellow peltate scales. *Chromosome number*, $2n = 32$, based on counts from roottips of seedlings, greenhouse progeny of Stone 2141 (DUKE).

Oreomunnea mexicana as here recognized constitutes a very natural assemblage. The range from Oaxaca, Mexico, to Cartago, Costa Rica, may at first appear to be rather exceptional, but not when viewed in light of the similarity in environmental conditions at each locality. All trees that I have seen, including ones from Mexico, Guatemala, Nicaragua, and Costa Rica, are invariably situated on steep hillsides and fog-shrouded ridges. Miranda (1946) vividly described this type of habitat for the Orizaba population: “. . . emergian de la sombra de la neblina y cuyas altas copas volvian a perderse en ella.” Present records indicate that the species ranges from 900 to 2600 m. There is reason to believe that the plants at higher elevations may not fare nearly so well as those growing in the 1000–1700 m

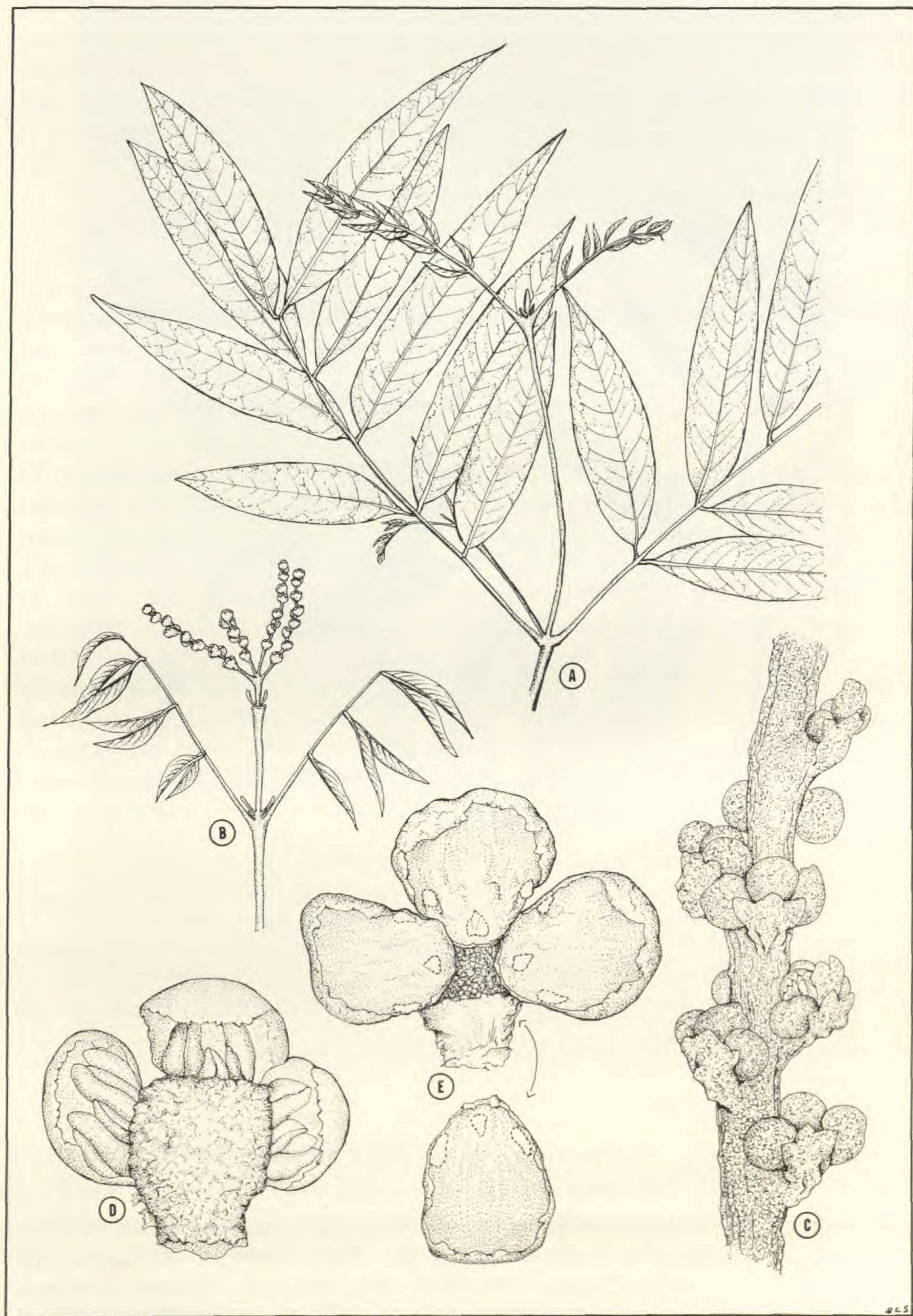


FIGURE 7. Vegetative and flowering features of *Oreomunnea mexicana* subsp. *mexicana*.—A. Shoot displaying decussate phyllotaxy (Stone 2141), $\times 0.4$.—B. Terminal staminate inflorescence (Stone 2141), $\times 0.4$.—C. Portion of staminate catkin (Stone 2144), $\times 6.5$.—D. Adaxial view of staminate flower (Stone 2144) with proximal sepal obscuring view of 3 stamens and receptacle, $\times 13$.—E. Adaxial view of staminate flower exposing attachment points of 12 stamens in two series (Stone 2144), $\times 13$.



FIGURE 8. Holotype of *Oreomunnea mexicana* subsp. *mexicana* (Rovirosa 1006, PH).

belt. Out of ten or so locations known for *O. mexicana* subsp. *mexicana*, only four have yielded flowering or fruiting specimens. These include: Rovirosa's type collection (fruits) from Chiapas (900–1000 m); Martinez (fruits) and Stone (male and female flowers and fruits) specimens from Oaxaca (1700 m); female flowers by Stone from Alta Verapaz, Guatemala (1300–1500 m); collections by Salas and Taylor (fruits) and Stone (flowers and fruits) from Jinotega and Matagalpa, Nicaragua (1450 m). A notation by Ross (Ross 55, US) that *O. mexicana*

is a "shrub in elfin forest" at 1500 m suggests that unfavorable exposures at even moderate altitudes may handicap growth and reproduction. Perhaps marginal populations are maintained through asexual means. I have observed, for example, that saplings of *O. mexicana* are capable of vegetative propagation. If the stem is prostrated on the ground, adventitious shoots may be stimulated. Also, it is quite likely that stump sprouts arise here as in *Alfaroa* (personal observation).

The geographical range of *Oreomunnea mexicana* has, to be sure, promoted varying degrees of population divergence, but the differences are subtle. Miranda (1946) thought he perceived a difference in the more numerous and sessile leaflets in the Orizaba specimens and indicated that he would later describe this element as a new species. However, no formal recognition was ever proposed, and, except for Molina's *Engelhardtia nicaraguensis* (1968), no other segregate or close relative has been recognized. The field characteristics of seedlings, saplings, and adult trees of *Oreomunnea mexicana* are remarkably distinctive and as far as I am aware uniform in all of the Middle American populations. Foliage of younger plants and sucker shoots on trees are typically reddish; the leaves are opposite, pinnately compound, and the leaflets are serrate. The larger trees can usually be spotted by the exfoliating bark that peels off in large strips (Fig. 6B). The leaflets on mature trees are mostly entire, but some serrate leaflets can always be found. *Alfaroa costaricensis* sensu lato (including *A. williamsii* Molina) is the only other species of tropical American Juglandaceae that approaches *O. mexicana* in this respect. The leaflets and terminal shoots of *O. mexicana* tend to be more slender than those of *O. pterocarpa* and the Alfaroas. This combination of characters unites the Mexican, Guatemalan, Nicaraguan, and Costa Rican populations of *O. mexicana*. Only in flower characters has it been possible to discern any significant differences. The following key emphasizes these differences in recognizing two subspecies.

KEY TO SUBSPECIES OF *OREOMUNNEA MEXICANA*

- Female flowers and fruits with conspicuous pedicels to 3 mm long; pistil oriented parallel to axis of catkin, sepals incurved; Mexico to Nicaragua 2a. subsp. *mexicana*
 Female flowers and fruits sessile or nearly so; pistil oriented at a 45° angle to axis of catkin, sepals spread; Costa Rica 2b. subsp. *costaricensis*

2a. Subspecies *mexicana*

Holotype: MEXICO. CHIAPAS: Hab. regione temperata locis humidis Andium Chiapensium, 900–1000 m, *Rovirosa 1006* (PH; photograph with two leaflets and several fruits, US).

Engelhardtia nicaraguensis Molina, Fieldiana Bot. 31: 358. 1968.

Type: NICARAGUA. MATAGALPA: Bosque nebulosa vecindades de Santa María de Ostuma, 1300 m, *Salas 2967* (F; isotype, EAP).

There are no vegetative features that I have found that can be used to recognize the subspecies. Thus, when the sterile specimens are cited it should be noted that provisional identification was based solely on geographic location. The female flowers of *Oreomunnea mexicana* have the only reliable diagnostic features. Subspecies *mexicana* has flowers with long pedicels and a bract-bracteole cup that curves to orient the pistil parallel to the axis of the catkin (Fig. 10H); in this respect it is reminiscent of the female flower of *Engelhardtia roxburghiana* (see Manning, 1940).

After careful examination of the type specimen of *Engelhardtia nicaraguensis* and a few subsequent collections, I can find no basis for recognizing this taxon. The female flowers (Fig. 10H) are indistinguishable from those of the Mexican (*Stone 2807*) and Guatemalan (*Stone 3003*) specimens. In the original description Molina (1968) did not single out any diagnostic features, but rather relied on a host of meristic differences between the type specimens:

	<i>E. mexicana</i>	<i>E. nicaraguensis</i>
Pairs of leaflets	3-4	4-6
Petiole length (cm)	1.5-2	2.5-3.5
Rachis length (cm)	2-6	4-9
Petiolule length (mm)	2-3	1-2
Leaflet length (cm)	5-8.5	3-8.5
Nut length (mm)	6-7	6-8

The inclusion of additional samples in this comparison completely blurs the distinctions noted above (see diagnostic descriptions under *O. mexicana*).

Fertile specimens: MEXICO. CHIAPAS: Hab. regione temperata locis humidis Andium Chiapensium, 900-1000 m, 24 Jul 1891, *Rovirosa 1006* (PH, holotype; US). OAXACA: Highway 175, 102.5 km S Valle Nacional, 1700 m, 7 Nov 1962, *Martinez 13-39* (MEXU, DUKE); highway 175, 42.1 km S Valle Nacional, 4900 feet, 16 Mar 1966, *Stone 2141* (DUKE); highway 175, 38.8 mi N Ixtlán de Juárez, 2 Feb 1971, *Stone 2807* (DUKE).

NICARAGUA. MATAGALPA: Bosque nebuloso vecindades de Santa María de Ostuma, 1300 m, May 1957, *Salas 2967* (F, holotype; EAP). JINOTEGA: Cerca de Aranjuez, 1160 m, Aug 1957, *Salas & Taylor 2967A* (EAP); near Santa María de Ostuma, on road to Aranjuez, 0.9 mi E of highway 3, 1450 m, 6 May 1966, *Stone 2181* (DUKE).

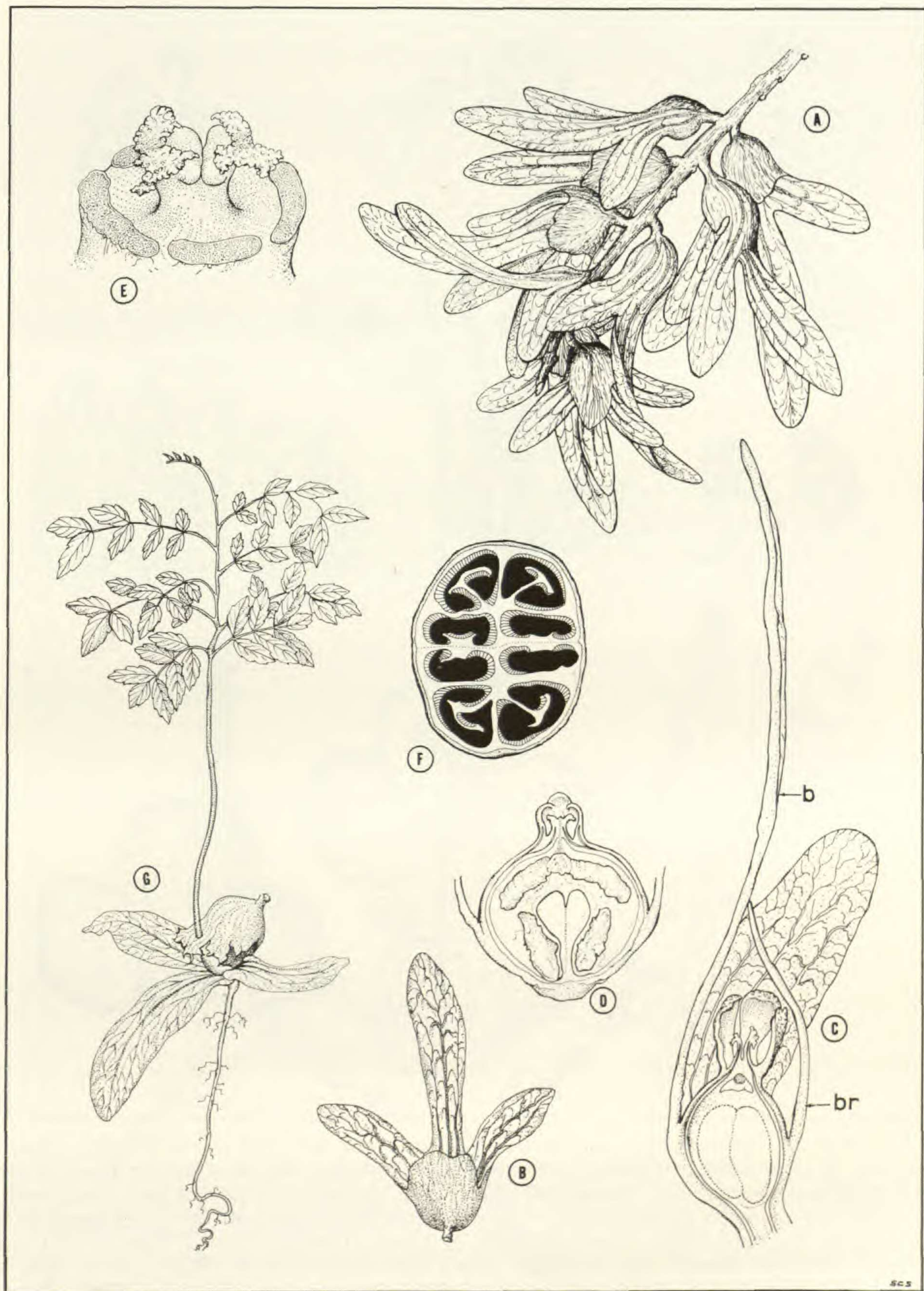
GUATEMALA. ALTA VERAPAZ: On highway 7E, 1.3 mi SE of highway 5 intersec. near Tactic, 25 May 1971, *Stone 3003* (DUKE).

Sterile specimens: MEXICO: VERACRUZ: Cerro de San Cristobal, near Orizaba, 4200-5000 feet, 3 Aug 1953, *Manning & Manning 53746* (A), 4 Aug 1953, *Manning & Manning 53770* (NY, PH), *Manning & Manning 53775* (DUKE), 8 Mar 1966, *Stone 2518, 2119, 2120, 2121, 2122, 2123, 2124* (DUKE); Santa Marta, 5000 feet, Los Tuxtlas range, 17 Jun 1963, *Ross 55* (US); near Ocotál Chico, 3000 feet, Los Tuxtlas, 24 Mar 1965, *Ross 120* (US); Ejido San Fernando, vertiente SW Sierra de Santa Marta, 1000 m, 14 Mar 1968, *Sousa 3551* (DUKE). OAXACA: Highway 175, 42.1 km S Valle Nacional, 4900 feet, 28 Jan 1965, *Stone 1872, 1873, 1875* (DUKE); highway 175, 42.1 km S Valle Nacional, 4900 feet, 2 Feb 1971, *Stone 2808, 2809, 2810, 2811, 2812* (DUKE).

GUATEMALA: ALTA VERAPAZ: Region of Chelac, NE of Carchá, 1500 m, 2 Apr 1939, *Standley 70379* (A, F); ridge SE of Tactic, 9 Nov 1969, *Stone 2697* (DUKE); highway 7E SE of Tactic, 2 km from junction with highway 5, 10 Nov 1969, *Stone 2703, 2704, 2705* (DUKE). BAJA VERAPAZ: Sierra de las Minas, E of Chilascó, 28 May 1950, *Lamb 113* (F, EAP). EL PROGRESO: Montaña Canahui, between Finca San Miguel and summit, 1600-2300 m, 10 Feb 1942, *Steyermark 43810* (A, F). GUATEMALA: No locality or date, *Aguilar 616* (F). HUEHUE-TENANGO: Cerro Huitz, Sierra de los Cuchumatanes, between Mimanjuitz and Yulhuitz, 1500-2600 m, 14 Jul 1942, *Steyermark 48619* (F).

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FIGURE 9. Fruits and seedling of *Oreomunnea mexicana* subsp. *mexicana*.—A. Inflorescence with terminally-borne fruits (*Stone 2141*), $\times 0.8$.—B. Adaxial view of mature fruit (*Stone 2141*) showing triveined wings and well-developed basal lobe, $\times 0.8$.—C. Radial section of fruit along secondary partition exposing two styler arms separated by major groove and enclosed by abaxial bract (b) and adaxial bracteoles (br) or basal lobe (*Stone 2141*), $\times 3.4$.—D. Radial section of fruit along primary partition exposing bifurcation of one styler



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arm by minor groove (*Stone 2141*), $\times 3.4$.—E. Polar view of horseshoe-shaped stigma on fruit, major groove oriented in north-south direction (*Stone 2141*), $\times 8.7$.—F. Transverse section of fruit at equator, oriented with primary partition in north-south direction: 8-celled, thin husk (outer dark band) and thin cartilaginous shell (stippled zone) (*Stone 2141*), $\times 3.4$.—G. Seedling displaying hypogeal germination, first aerial leaves opposite and compound, succeeding leaves alternate (*Stone 2142*), $\times 0.8$.

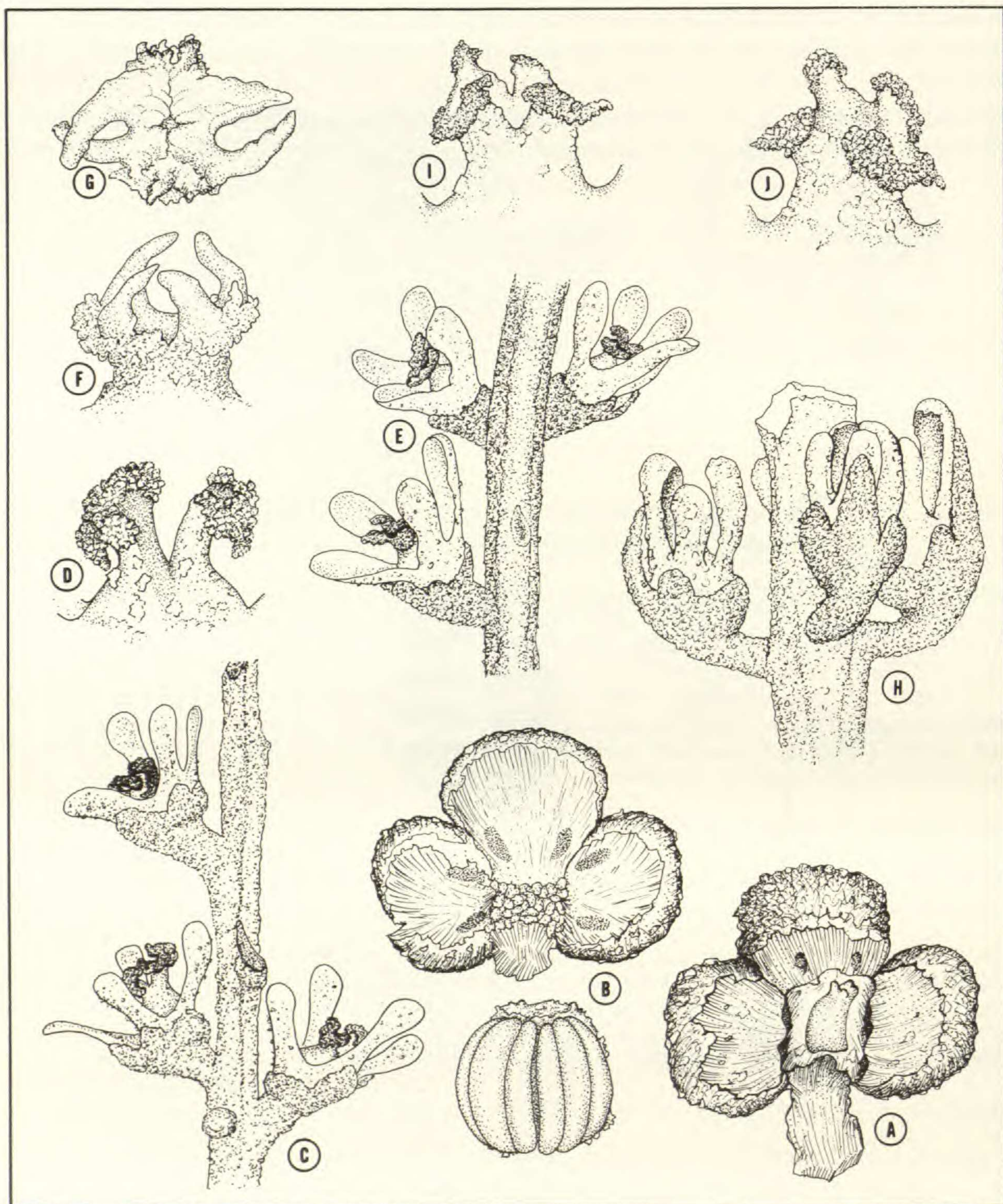


FIGURE 10. Inflorescence and flowers of *Oreomunnea mexicana*: A, C–G, subsp. *costaricensis*; B, H–J, subsp. *mexicana* (Nicaragua).—A. Adaxial view of staminate flower with 8 stamens and aborted pistil (Stone 2680), $\times 15$.—B. Adaxial view of staminate flower with 8 stamens in one series (Stone 2181), $\times 15$.—C. Pistillate flowers with spreading sepals and moderately-developed stigma (Stone 2177B), $\times 6.5$.—D. Carinal stigma (Stone 2177B), $\times 18$.—E. Pistillate flowers with spreading sepals and well-developed stigma (Stone 2680), $\times 6.5$.—F. Side view of stigma sighting along major groove (Stone 2680), $\times 18$.—G. Polar view of stigma (Stone 2680), $\times 18$.—H. Pistillate flowers with incurved sepals (Stone 2181), $\times 5.1$.—I–J. Side view of carinal stigma (Stone 2181), $\times 18$.



FIGURE 11. Androgynous panicle of *Oreomunnea mexicana* subsp. *costaricensis* (Stone 2680), $\times 2.1$.

2b. Subspecies *costaricensis* Stone, subsp. nov.

Flores feminei pedicellis brevibus et calycum lobis reflexis.

Type: COSTA RICA. CARTAGO: 4 km S of Muñeco, ridge between Río Patarrá and Río Sombrero, *Stone 2680* (DUKE).

This new subspecies is known only from Cartago Province, Costa Rica. While it grows in the same general areas as *Oreomunnea pterocarpa*, *Alfaroa costaricensis*, and *A. manningii*, *O. mexicana* subsp. *costaricensis* is usually situated above the protected ravines on fog-shrouded mountain ridges in a premontane rainforest (*sensu* Holdridge, 1964). No good fruiting material has been collected, although remnants of the winged bracts were found attached to young seedlings. The female flowers are somewhat smaller than those of *O. mexicana* subsp. *mexicana*, in addition to the fact that the pedicel is short, the pistil is oriented at a 45° angle to the axis of the catkin, and the sepal lobes are spread and rather flat. There appears to be some variation in the extent of elaboration of the stylar arms. The material from Valle Escondido (*Stone 2177B*) has a deep stylar cleft, but only

moderately developed minor grooves on the stigma lobes (Figs. 10C–D). Specimens from Muñeco (*Stone 2680*) have deep minor grooves that give the stigma a pronounced 4-pronged appearance (Figs. 10E–G). The significance of these differences cannot be evaluated until more collections are available.

Fertile specimens: COSTA RICA. CARTAGO: Ridge above Valle Escondido, ca. 14 km NE of Tuís, 1100 m, 29 Apr 1966, *Stone 2177B* (DUKE); 4 km S of Muñeco, ridge between Río Patarrá and Río Sombrero, 29 Aug 1968, *Stone 2680* (DUKE, holotype).

Sterile specimens: COSTA RICA. CARTAGO: Valle Escondido, ca. 14 km NE Tuís, 1100 m, 1966, *Hatheway* (DUKE), 29 Apr 1966, *Stone 2177A* (DUKE); Tapantí, 1300 m, 2 Sep 1966, *Hatheway* (DUKE), 6 Nov 1967, *Stone 2316, 2317, 2318* (DUKE), 20 Jan 1968, *Stone 2334A, 2335* (DUKE); ridge above Tapantí on precipitous road to Tausito, 4500 feet, 23 Mar 1968, *Stone 2342, 2343* (DUKE), 13 Nov 1969, *Stone 2718, 2718A* (DUKE), 8 Jun 1970, *Stone 2745, 2746* (DUKE); Muñeco on Río Navarro, 1400–1500 m, 6–7 Mar 1926, *Standley & Torres 50969* (US); La Estrella, 26–27 Mar 1924, *Standley 39446* (US); 4 km S of Muñeco on knoll between Río Patarrá and Río Sombrero, 24 Mar 1968, *Stone 2351* (DUKE); ca. 5 km S of Muñeco, above Río Sombrero, 9 Jun 1970, *Stone 2750* (DUKE).

LITERATURE CITED

- BAKER, H. G. 1959. Reproductive methods as factors in speciation in flowering plants. Cold Spring Harbor Symp. Quan. Biol. 24: 177–191.
- . 1963. Evolutionary mechanisms in pollination biology. *Science* 139: 877–883.
- CANDOLLE, C. DE. 1862. Mémoire sur la famille des Juglandées. *Ann. Sci. Nat. Bot.* IV. 18: 5–48.
- . 1864. Juglandaceae. In “*Prodromus systematis universalis regni vegetabilis*.” 16: 134–146.
- . 1914. *Engelhardtia Oreomunnea* C. DC. Une espèce remarquable du Costa-Rica. *Bull. Soc. Bot. Genève* II. 6: 165–170.
- CONDE, L. F. & D. E. STONE. 1970. Seedling morphology in the Juglandaceae, the cotyledonary node. *Jour. Arnold Arbor.* 51: 463–477.
- EICHLER, A. W. 1878. Juglandaceae. In “*Blütendiagramme*.” Vol. 2. Leipzig.
- HEIMSCH, C., JR. & R. H. WETMORE. 1939. The significance of wood anatomy in the taxonomy of the Juglandaceae. *Amer. Jour. Bot.* 26: 651–660.
- HJELMQVIST, H. 1948. Studies on the floral morphology and phylogeny of the Amentiferae. *Bot. Not.* 2: 5–171.
- HOLDRIDGE, L. R. 1964. *Life Zone Ecology*. San José, Costa Rica.

- JACOBS, M. 1960. Juglandaceae. In C. G. G. I. van Steenis (editor), "Flora Malesiana I." 6: 143–154.
- LEROY, J. F. 1951. Pour la réhabilitation du genre *Oreomunnea* Oersted (Juglandacées). Bull. Mus. Hist. Nat. (Paris) Sér. 2. 23: 126–127.
- . 1955. Étude sur les Juglandaceae. Mém. Mus. Natl. Hist. Nat., Sér. B. Bot. 6: 1–246.
- MACGINITIE, H. D. 1969. Juglandaceae. In "The Eocene Green River Flora." Univ. Calif. Publ. Geol. Sci. 83: 94–95.
- MANNING, W. E. 1938. The morphology of the flowers of the Juglandaceae. I. The inflorescence. Amer. Jour. Bot. 25: 407–419.
- . 1940. The morphology of the flowers of the Juglandaceae. II. The pistillate flowers and fruits. Amer. Jour. Bot. 27: 839–852.
- . 1948. The morphology of the flowers of the Juglandaceae. III. The staminate flowers. Amer. Jour. Bot. 35: 606–621.
- . 1949. The genus *Alfaroa*. Bull. Torrey Bot. Club 76: 196–209.
- . 1959. *Alfaroa* and *Engelhardtia* in the New World. Bull. Torrey Bot. Club 86: 190–198.
- . 1966. New combinations and notes on *Engelhardtia* (Juglandaceae) of the Old World. Bull. Torrey Bot. Club 93: 34–52.
- METCALFE, C. R. & L. CHALK. 1950. Anatomy of the Dicotyledons. Vol. 2. Oxford.
- MIRANDA, F. 1946. El género *Engelhardtia* de Orizaba, Ver. Soc. Bot. Mexico Bot. 4: 15–16.
- MOLINA, A. 1968. Two new Nicaraguan Juglandaceae. Fieldiana, Bot. 31: 357–359.
- NAGEL, K. 1914. Studien über die Familie der Juglandaceen. Bot. Jahrb. Syst. 50: 459–530.
- OERSTED, A. S. 1856. Plantae novae centroamericanae. Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 3: 33–43.
- . 1870a. Bidrag til Kundskab om Valdnødplanterne. Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1870: 159–173.
- . 1870b. Notice sur les Juglandees. Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1870: 1–3. [Pagination not sequential; 3-page text contains comments on plates of 1870: 159–173.]
- PITTIER, H. 1957. Plantas usuales de Costa Rica. 2nd ed. rev. Univ. Costa Rica, Ser. Ci. Nat. 2. [*Oreomunnea* was not listed in the 1908 edition, although Pittier referred to *O. pterocarpa* in his "Introduction"; the compilation of information and photograph of fruits in the revised edition were added by M. Quiros.]
- STANDLEY, P. C. 1927a. The American species of *Engelhardtia*. Trop. Woods 12: 12–15.
- . 1927b. *Alfaroa*, a new genus of trees of the family Juglandaceae from Costa Rica. Jour. Washington Acad. Sci. 17: 77–79.
- . 1937. Juglandaceae. In "Flora of Costa Rica." Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 372–373.
- . 1940. Juglandaceae. In "Studies of American plants—IX." Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 12–13; 225.
- STONE, D. E. 1968. New World Juglandaceae: a new species of *Alfaroa* from Mexico. Amer. Jour. Bot. 55: 477–484.
- . 1970. Evolution of cotyledonary and nodal vasculature in the Juglandaceae. Amer. Jour. Bot. 57: 1219–1225.
- WHITEHEAD, D. R. 1965. Pollen morphology in the Juglandaceae, II: Survey of the family. Jour. Arnold Arbor. 46: 369–410.
- WILLIAMS, L. O. & A. MOLINA. 1970. The Juglandaceae of Guatemala. Fieldiana 32: 207–209.
- WOLFE, J. A. 1957. Tertiary Juglandaceae of Western North America. M.A. Thesis, Univ. Calif., Berkeley [unpubl.]

EDITOR'S NOTE

The first eleven papers in this issue of the ANNALS were presented at the symposium "Plant Species Disjunctions, their Significance and Methodological Approaches." The symposium was co-sponsored by the American Bryological and Lichenological Society, the American Fern Society, the Pteridological and Systematic Sections of the Botanical Society of America, and the American Society of Plant Taxonomists. It was held at the joint meeting of the Canadian Botanical Society and the American Institute of Biological Sciences at Edmonton, Alberta, in June 1971.

The revolution in geological sciences brought about in the past few years by theory of plate tectonics affects the interpretation of many plant disjunctions. Biologists must constantly keep in mind not only past positions of continents when studying disjunctions, but factors affected by the position of continents, such as climate, must also be considered. The cover banner on this issue of the ANNALS is simplified from one of Alfred Wegener's reconstructions in the fourth edition of his *Die Entstehung der Kontinente und Ozeane* (an English translation by John Biram is available from Dover Publications). The three views show, from left to right, the Americas, Africa, and Europe in the Upper Carboniferous, Eocene, and Lower Quaternary.—*Editor*.

THE FIFTH ANNUAL JESSE M. GREENMAN AWARD

The 1972 Greenman Award was presented at the Annual Banquet of the Botanical Society of America to William T. Gillis, Arnold Arboretum. The award winning publication is an exhaustive, broadly systematic study of two sections of *Toxicodendron*, "The systematics and ecology of poison-ivy and the poison-oaks (*Toxicodendron*, Anacardiaceae)" (*Rhodora* 73: 72-159; 161-237; 370-443; 465-540. 1971).

The Award of \$250 is presented each year by the Alumni Association of the Missouri Botanical Garden. It recognizes the best paper in plant systematics based on a doctoral dissertation published during the *previous* year. Papers published in 1972 are now being considered. Reprints of such papers should be sent to Peter H. Raven, Director, Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110, before 1 May 1973.—*Editor*.

The previous issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, Vol. 59, No. 1, pp. 1-104, was published on 27 July 1972.